Is silviculture able to enhance wild forest mushroom resources? Current knowledge and future perspectives

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Abstract

Fungal fruit-bodies are an important economic resource both for recreational pickers and commercial markets. The broad interest in forest fungi and mushrooms has motivated attempts to develop appropriate silvicultural methods able to preserve and improve mushroom yields. Defining best practices for the sustainability and profitability of forest fungal resources is the main aim of 'mycosilviculture'. However, the difficulty of monitoring and studying such a cryptic kingdom (i.e., fungi) under real forest conditions has led to rather scattered scientific knowledge of the effects of forest management regimes and silvicultural operations on wild mushroom resources. Here, we review the current scientific literature regarding the influence of (i) stand characteristics, i.e. stand age, stand density, canopy cover and tree species composition, (ii) silvicultural practices and (iii) other management-related disturbances affecting the yield of wild epigeous mushrooms, with the aim of systematizing existing scientific knowledge and identifying gaps in knowledge in order to suggest future lines of research. Most of the research in the field of mycosilviculture to date has focused on ectomycorrhizal mushrooms, which include the majority of wild commercial mushrooms. The main findings from the literature indicate that forest management practices, by modifying stand characteristics and microclimatic conditions, can influence wild mushroom occurrence and productivity, both positively and negatively, depending on the specific fungal ecological needs, reproductive strategies, forest type and management regime. Further research efforts relating to all aspects of the interaction between forest management, fungal ecology and mushroom production are needed: in particular, additional research efforts should be devoted to understanding mushroom yield dynamics in uneven-aged and mixed forests and evaluating the effects of regeneration methods on fungal communities.

Keywords

Mycosilviculture; yield; mushrooms; forest management; fungi.

1. Introduction

Fungi are widely recognized as fundamental components of biodiversity and ecosystem functioning. Furthermore, fungal fruit-bodies, which constitute the main resource of an important socioeconomic activity based on mushroom picking for both recreational purposes and commercial markets, provide important provisioning and cultural ecosystem services to society. The commercial value of mushrooms can exceed 40 million euros (€) in countries such as Italy (ISTAT, 2008) or 32 million € in regions such as Catalonia (Bonet et al., 2014). The value derived from mushrooms is even higher if we also consider the recreational value of mushroom picking as a leisure activity (Martínez de Aragón et al., 2011; Latorre, 2016). Indeed, the economic profit from wild mushrooms can be higher than timber revenues (Palahí et al., 2009; Pettenella and Secco, 2006), especially in areas where timber production is not very profitable. Furthermore, the economic profit from wild mushrooms can represent a considerable percentage (up to 25%) of the soil expectation value, even in countries such as Finland where timber production is an important economic activity (Tahvanainen et al., 2016). De Roman and Boa (2006) calculated that a family of four people living in a rural area of Northern Spain can derive profits of 5,600–8,400 € from picking saffron milk caps (*Lactarius deliciosus s.l.*) over the course of a season. In Eastern Finland, Cai et al. (2011) reported that the seasonal earnings of professional pickers were 1,224 euro (more than 5% of the average net annual household income in Finland) and more recently Sisak et al. (2016) reported that three quarters of the rural households in the Czech Republic collect Non Wood Forest Products (NWFPs) (mainly mushrooms and berries). However, quantifying the exact contribution of mushrooms to household incomes in economic terms may still be underestimated due to the difficulty in accurately estimating the amount of wild mushrooms that are sold (because the economy is largely informal) (Maso, 2008).

The twofold importance of wild forest mushrooms in ecological and socioeconomic terms underlines the need for promoting and preserving this resource (Dettori et al., 2009). For these reasons, forest management regimes oriented toward the provision of wild mushrooms need to be based on reliable quantifications of the impact of anthropogenic disturbances on mushroom yields, which also implies an in depth scientific knowledge of the key drivers that affect fungal communities.

Sporocarp production has been the focus of many studies (Vogt et al., 1992) and numerous variables influencing mushroom production have been identified. In addition to specific plant–fungal interactions, other key factors affecting sporocarp emergence include climatic conditions and soil and topographical characteristics (Figure 1). Water availability is fundamental for fruit-body formation (Wiklund et al., 1995; Ogaya and Peñuelas, 2005; Büntgen et al., 2012). In particular, mean monthly precipitation and accumulated mean monthly evapotranspiration are strongly related to annual fruit-body production (Martínez de Aragón et al., 2007; Taye et al., 2016). Climatic conditions may also affect mushroom production in the long term (Gange et al., 2007; Kauserud et al., 2008; Ágreda et al., 2016) as a consequence of climate change. However, climatic or site conditions alone do not completely explain mushroom occurrence (Barroetaveña et al., 2008; Egli et al., 2011; Krebs et al.,

2008) because the interactions between individual meteorological variables and other ecosystem variables are quite complex (Egli et al., 2011).

Stand structure characteristics (e.g., tree species composition, stand age, and stand density) influence mushroom yields (Figure 1). Identifying stand characteristics that enhance the productivity of edible and marketable wild mushrooms is also the basis for the development of decision-support tools based on predictive models, which are being used to select optimal forest management alternatives for the provision of multiple ecosystem services, e.g., the joint production of mushrooms and timber (Palahí et al., 2009; Tahvanainen et al., 2016).

(FIGURE 1 HERE)

The growing interest in mushroom production has led to the development of a promising new discipline over the past few decades: "mycosilviculture". According to Martínez-Peña et al. (2011), mycosilviculture attempts to integrate timber and mushroom production into the management of forest ecosystems. However, a broader, more generalized definition of mycosilviculture based on existing formal definitions of silviculture (e.g., Ciancio, 1981; Ciancio and Nocentini, 1997) is: the experimental science studying the interactions between the natural dynamics of forest ecosystems and management techniques, with the aim of defining the best practices for the sustainability and profitability of fungal resources.

Although the best practices necessary for truffle (*Tuber* spp.) cultivation are well established (e.g., Bonet et al., 2009; Giovannetti et al., 2010; Reyna and Garcia-Barreda, 2014), this is not the case for epigeous macromycetes, some of which are also commercially important. Most of the economically valuable species are mycorrhizal fungi (e.g. *Boletus* spp., *Lactarius* spp., *Cantharellus* spp. and *Tricholoma* spp.). However, some saprotrophic (e.g. *Morchella* spp., *Agaricus* spp. and *Macrolepiota* spp.) and parasitic (e.g. *Armillaria* spp.) species may also be important for local economies (Table 1). Although an increasing number of studies have focused on evaluating the effects of silvicultural practices on fungal yield in recent years (e.g., Bonet et al., 2012; Lin et al., 2015), and some authors have proposed guidelines for fungal-oriented silviculture (Palahí et al., 2009; Pierangelo and Rolland, 2013; Bettini et al., 2016), the large number of potential variables influencing mushroom yields, and their interdependence, make the development of clear forest management recommendations rather challenging. Moreover, the existing studies are mostly local or regional and, hence, the scientific knowledge on this topic is rather scattered. Therefore, recommendations that may be useful for a specific area may not be suitable for sites with a different climate or forest stand structure, or if the highly valued edible mushroom species differ between regions according to differences in stakeholders' preferences. In this sense, a systematic review of current knowledge about forest management practices that are able to increase mushroom yield may help to shed light on this complex issue and contribute to clarifying the state of the art as a basis for further research.

(TABLE 1 HERE)

Based on these considerations, the aims of this paper are: (i) to review the current scientific literature regarding the effects of forest management on the yield of wild epigeous mushrooms, with a particular focus on those that are mainly used worldwide as a food provisioning ecosystem service and that are also linked to the provision of cultural ecosystem services (recreation and tourism) (Table 1); and (ii) to identify gaps in our knowledge and suggest new research lines.

Following this introduction, Section 2 reviews the stand variables that are known to affect mushroom production, i.e., forest age, stand density, canopy cover and tree species composition. Section 3 deals with the forest management practices that may influence wild epigeous mushroom occurrence by modifying stand characteristics and microclimatic conditions i.e., the effect of thinning, regeneration methods and other management practices and anthropogenic disturbances (i.e., logging, mushroom picking, trampling, raking, shrub control and prescribed fire). Lastly, Section 4 summarizes the main findings from the literature review, discusses gaps in our knowledge and recommends areas for future research.

2. Stand structure variables influencing mushroom production

2.1 Forest stand age

Studies have shown that forest age is an important factor in mushroom fruiting abundance. However, the ecology of fungal species can vary considerably even within the same genus and, therefore, providing a general overview of the results is difficult. Indeed, wild mushrooms can be classified as typical of either early- or late-stage forest succession (Mason et al., 1987) according to their physiology and nutritional requirements (Dighton and Mason, 1985), although some species can be present in both early and late successional stages: e.g., *Suillus granulatus* in pine forests (Savoie and Largetau, 2011). Furthermore, the concept of an 'old' or 'young' stand may depend, e.g., on the fertility of the site or the longevity of the tree species (Martínez-Peña et al., 2012a). For these reasons, mushroom fruiting can vary depending on forest type and fungal species.

Many studies agree that sporocarps of mycorrhizal fungi are more abundant in younger stands. This evidence has been related to the physiological status (higher growth rate) of trees in early stage stands (Senn-Irlet and Bieri, 1999; Bonet et al., 2008; Egli et al., 2010; Tahvanainen et al., 2016). For example, sporocarp production in young and open *Picea excelsa* stands was almost double that of older stands (Senn-Irlet and Bieri, 1999). In a study conducted in mixed-coniferous forests in Russia, Chibisov and Demidova (1998) reported that mushroom production was greatest in young stands (15–35-years-old). In Finland, a study on mushroom yields in pine forests of different ages reported that the 20–30-year-old stands produced greater quantities of sporocarps than the other stands (Hintikka, 1988). Similar results have been found by Kalamees and Silver (1988) in *Pinus sylvestris*-dominated stands, where both total and edible mushroom yields were greater in 25-year-old stands than in other stands. Smith et al. (2002) found that the average epigeous sporocarp yield in *Pseudotsuga menziesii* forests in Oregon (USA) was about six times lower in very old (more than 400 years old) stands compared with young and rotation-age stands.

Similar findings have been reported regarding the productivity of important edible, marketable species such as *Lactarius deliciosus s.l.*. Martínez de Aragón et al. (2007) reported that *Lactarius sanguifluus* sporocarps were more abundant in young forest stands (<50 years old) and that although stand age was not correlated with total sporocarp yield, it was negatively associated with the amount of saffron milk caps. This group of species is mainly found in conifer stands that are less than 40 years old (Fernández-Toirán et al., 2006; Kranabetter et al., 2005; Kucuker and Baskent, 2015). Furthermore, the results of a 15-year study monitoring mushroom production in *Pinus pinaster* stands in Central Spain revealed that saffron milk caps were found in all age classes, but that significantly higher yields were obtained in the youngest stands (11–20 years old) (Ágreda et al., 2014). In a similar study, Martínez-Peña et al. (2012a) reported that the *L. deliciosus* sporocarp yield peaks twice in stands dominated by Scots pine: the first peak in yield occurs in stands that are between 16 and 30 years old and then again when the stand is more than 71 years old. The authors suggested that these findings reflect the preference of this species for open-canopy conditions, which can also be found within mature stands in intensively managed forest ecosystems.

The influence of stand age on the production of *Boletus edulis s.l.* has also been studied. Keizer and Arnolds (1994) reported that this species group was found more frequently in 20- to 40-year-old *Quercus* and *Fagus* forests than in younger (i.e., 10–20-year-old) and older (50–140-year-old) forests. Higher yields of *B. edulis* have also been reported in mature pine stands (Hintikka, 1988; Keizer and Arnolds, 1994). For example, Martínez-Peña et al. (2012a) found that *B. edulis* sporocarp production was greater in 51–70-year-old *Pinus sylvestris* stands than in younger stands. In Norway spruce

(*Picea excelsa*) stands, *B. edulis* sporocarp production reaches its highest levels 25–30 years after planting, just before the first thinning usually takes place (Tahvanainen et al., 2016).

Ortega-Martínez et al. (2011) evaluated the effect of forest age on the weekly growth of sporocarps, and reported that both *B. edulis* and *L. deliciosus* fruit-bodies grow faster when they are associated with young Scots pine trees (<30-years-old). Sporocarps were larger and nearly 50% heavier compared with mushrooms of the same species growing in older pine stands, which may be because young *Pinus sylvestris* trees require more nutrients to support their rapid growth rates during the early stand development stage, and the ectomycorrhizal fungi may benefit from the higher carbohydrate allocation to the root system. By contrast, American Matsutake (*Tricholoma magnivelare*) is generally found in mature stands that are more than 70 years old (Kranabetter et al., 2002; 2005).

2.2 Forest stand density and canopy cover

The composition of the mycorrhizal fungal community is strongly influenced by forest stand structure and density owing to their close symbiotic relationship with trees (Santos Silva et al., 2011). Stand basal area is one of the most used variables to describe the density of forest stands and is a strong predictor of fungal yield (e.g., Bonet et al., 2008; 2010; de-Miguel et al., 2014; Tahvanainen et al., 2016).

In *Pinus sylvestris* stands in the Central Pyrenees, Bonet et al. (2008) found that maximum mushroom yield was achieved under stand basal areas of approximately 20 m^2 ha^{-1}. Similar findings have been reported from a study based on 21 plots established in *Pinus halepensis*, *Pinus nigra* and *Pinus sylvestris* stands in Northeastern Spain (Bonet et al., 2010): maximum productivity of total, edible and marketable mushrooms was recorded in low–medium density stands with stand basal areas ranging from 15 to 20 m^2 ha^{-1}. More recently, de-Miguel et al. (2014) reported that the optimal stand basal area that maximizes edible and marketable mushroom yield may differ among Mediterranean pine forest ecosystems (i.e., pure *P. sylvestris*, *P. nigra*, *P. halepensis* and *P. pinaster* stands, and mixed *P. sylvestris–P. nigra* and *P. nigra–P. halepensis* stands), ranging between 10–15 m^2 ha^{-1} in pure *P. halepensis* stands (growing under rather arid conditions) and 35–40 m^2 ha^{-1} in pure *P. pinaster* stands growing under good conditions.

Martínez-Peña et al. (2012b) determined that stand basal area affects *Boletus edulis* yield, with productivity predicted to peak in the *P. sylvestris* forests of Central Spain when the stand basal area is approximately 40 m^2 ha^{-1}. Tahvanainen et al. (2016) have also identified the optimal stand basal area that maximizes the production of *B. edulis* (approximately 25 m^2 ha^{-1}) and *Lactarius* spp. (approximately 30 m^2 ha^{-1}) in Norway spruce stands in Finland.

Stand density can also be described by the number of trees per hectare. However, this alternative quantification of density seems to be less relevant than stand basal area for understanding mushroom occurrence and yield. For example, Kucuker and Baskent (2015) found that this variable was not useful for predicting the occurrence of two *Lactarius* species (*L. deliciosus* and *L. salmonicolor*) in the Kızılcasu Planning Unit, Turkey.

Canopy cover is also linked to forest stand density, and its effect on fungal yield has been studied in various forest ecosystems. Stands without canopy closure seem to be more suitable for mushroom production, especially in the case of important edible and marketable species such as *Lactarius deliciosus s.l.* and *Boletus edulis s.l.* For example, Ágreda et al. (2014) reported that *L. deliciosus* benefits from open stands because mushroom yields were higher in young forests without canopy closure than in forests with canopy closure. Martínez-Peña et al. (2012a) also reported higher *Lactarius* yields in open stands – both young and old – than in closed stands. These findings were supported by a Turkish study (Kucuker and Baskent, 2015): if canopy closure increases, the probability that *L. deliciosus* and *L. salmonicolor* sporocarps will be absent also increases. These authors hypothesized that canopy closure has an effect on soil temperature and moisture. Even *Boletus edulis* may benefit from stands without total canopy closure (Salerni and Perini, 2004). Likewise, in

Cistus ladanifer shrublands, a canopy cover of, for example, 80% supports sporocarp emergence better than total closure (Hernández-Rodríguez et al., 2015a).

2.3 Tree species composition

There is a strong relationship between macrofungal communities and vascular plant composition (e.g., Barluzzi et al., 1992; Packham et al., 2002; Landi et al., 2015), and the effect of tree species composition on the fungal community can be stronger than the influence of soil properties (Urbanová et al., 2015). This is partly due to the preference of some ectomycorrhizal species for specific host trees, as well as to differences in the litter properties and tree debris (i.e., needles, leaves, and cones) in the case of saprotrophic fungi (Zhou and Hyde, 2002).

Fungal species can be either generalists or specialists, depending on their ability to establish mycorrhizal associations with different tree species under a wide range of growing conditions or only with a given tree species under a particular range of environmental conditions, respectively. In the Holarctic realm, most ectomycorrhizal fungi are usually associated with several host trees (Kennedy et al., 2003). However, some important exceptions have been identified. *Suillus* and *Rhizopogon* genera are *Pinaceae*-specific fungi (Molina and Trappe, 1982). Furthermore, there are many symbionts that are exclusively associated with *Alnus* tree species (Molina, 1979; Tedersoo et al., 2009). Host specificity may be found not only at the genus level but also at the species level. For example, *Lactarius deterrimus*, which show a clear preference for Norway spruce under temperate conditions (Buée et al., 2011). Among important marketable species, *L. deliciosus s.l.* forms mycorrhizae with several Pinaceae species, whereas *Boletus edulis* and *Cantharellus* spp. are more generalist species that may establish symbioses with several coniferous and broadleaf tree species at different latitudes and altitudes. Some of the tree species associated to these prized marketable mushrooms are commonly used in reforestation (e.g. *Pinus*, *Picea*, *Pseudotsuga*, *Abies*) in the northern hemisphere and can produce relevant revenues from timber. This facilitates co-management of timber and mushrooms.

While it is accepted that fungal diversity increases with increasing tree species richness (Landi et al., 2014), the effect of tree composition on mushroom production is less clear. In this regard, Weigand (1997) reported that the productivity of *Tricholoma magnivelare* can be enhanced by between 100% and 400% by changing the tree composition and increasing the presence of American Matsutake host trees. In a long-term experiment in mixed forests, Egli et al. (2010) showed that the productivity of host-specific epigeous mushrooms is strongly related to the relative abundance of the host tree, which can be influenced through silviculture.

3. Effect of forest management practices

3.1 Thinning

Thinning is the removal of a number of trees within a stand with the aim of enhancing the growth of the remaining trees by reducing the competition between them. As a man-induced disturbance of forest ecosystems, it may affect biodiversity and other related ecosystem functions (Bengtsson et al., 2000), including fungal communities (Lin et al., 2015), especially if combined with other environmental drivers (Tedersoo et al., 2011) such as climate factors (Kauserud et al., 2008). Since thinning modifies the humidity and light penetration under the canopy, thinned stands may experience more accelerated wetting and drying of the forest soil (Pilz and Molina, 2002). This can lead to a change in the presence and abundance of fungal species based on their specific temperature and water requirements. Furthermore, by removing the associated host trees, thinning may also eliminate some mycorrhizal fungi that were colonizing tree roots. At the same time, several mycorrhizal fungi associated to released trees may thrive (Bonet et al., 2012). The increased growth of the remaining trees may result in an increased allocation of carbohydrates to the mycorrhizal fungi, which, in turn, may partly aid them in the production of carpophores, i.e., healthy stands have a tendency to produce more mushrooms of ectomycorrhizal fungal species than weak and slow-growing trees (Savoie and Largetau, 2011). Therefore, the net effect of thinning on mycorrhizal mushroom yields, at least in the short-term, is the result of the trade-off between immediate reduction in colonies and increased production of remaining mycorrhizal fungi.

In addition, there may be an increase in fruitbody production of non-mycorrhizal species after thinning, including both saprotrophic-terricol and saprotrophic-lignicolous species, as shown by Egli et al. (2010) in a long-term experiment in Switzerland. However, Kim et al. (2010) reported no difference in the occurrence of *Armillaria* spp., a very common and appreciated edible group of parasitic species, in thinned stands compared to unthinned stands.

The influence of thinning on fruitbody abundance can even be seen the first year after thinning (Bonet et al., 2012), although various studies have reported that thinning can have very different effects (i.e. either positive or negative) on mushroom yields. Normally, mushroom production seems to decrease after the disturbance (Pilz et al., 2006; Egli et al., 2010). However, Bonet et al. (2012) showed that *Lactarius deliciosus s.l.* yields were higher in thinned stands than in unthinned stands from the first productive season after the silvicultural cut, probably due to the low impact of the forest harvest operations in the forest area. Kropp and Albee (1996) also reported a similar trend for the same mushroom species in *Pinus contorta* stands and Tahvanainen et al. (2016) suggested that thinning would promote *B. edulis* yields in spruce plantations in Finland. A significantly positive correlation between fruitbody production (number of sporocarps) and tree-ring width was also shown in a thinned mixed forest (Egli et al., 2010) and in a dry *Pinus pinaster* ecosystem (Primicia et al., 2016).

However, some authors have reported that thinning has a negative impact on mushroom resources, with a decline in sporocarp production regardless of tree removal intensity, even if this effect varied by season (Luoma et al., 2004). Pilz et al. (2006) also found that the number and biomass of a chanterelle species (*Cantharellus formosus*) significantly decreased in the first year after thinning, even if no differences were observed in the mid-term (six years after treatment).

These contradictory results may be explained by the fact that thinning does not have the same effect on all species. Effects are adverse or positive depending on the specific ecological needs of different fungal species, their reproductive strategies and forest type (Pilz and Molina, 2002; Buée et al., 2005). Kropp and Albee (1996) demonstrated that species of the genus *Suillus* (*Suillus brevipes*, *Suillus tomentosus*) appear to be favored by changes resulting from silvicultural practices. *L. deliciosus* also benefits from open stands, so thinning can positively influence its productivity (Bonet et al., 2012). However, certain groups of ectomycorrhizal fungi (in particular the Hygrophoraceae) are negatively affected by even low-intensity thinning (Kropp and Albee, 1996). The productivity of *Cantharellus* species, which requires wet conditions to produce fruitbodies, seems to be reduced in fast-drying soils after thinning (Pilz et al., 2006). After a silvicultural intervention in a 12-year-old Scots pine plantation, Shaw et al. (2003) reported that only three ectomycorrhizal species (*Suillus bovinus*, *Gomphidius roseus* and the not-edible *Cortinarius semisanguineus*) out of 19 considered in the study showed an increase in sporocarp production.

Thinning may also influence the availability of host trees for target species (Landi et al., 2015) by selecting particular tree species: preserving host trees that are suitable for target species may increase the production of mushrooms, as demonstrated by Weigand (1997) for *Tricholoma magnivelare*.

Thinning intensity often varies according to different silvicultural objectives and can influence mushroom production. Various levels of thinning intensity can be identified based on the quantity of trees removed. Thus, in light thinning, the reduction in the stand basal area is usually less than 15–20%, while in high-intensity thinning, the stand basal area may be reduced by more than 35–40% (Mäkinen and Isomäki, 2004). Medium-intensity thinning has been reported to be preferable to improve mushroom yields. Salerni and Perini (2004) observed that a greater amount of *B. edulis* sporocarps were obtained from forest stands undergoing moderate thinning (removal of approximately 20% of the stand basal area). Egli and Ayer (1997) demonstrated that a 35% reduction of stems in a mixed forest in Switzerland increased edible mushroom production up to six-fold.

Conversely, heavy thinning, characterized by basal area removal ranging from 40% up to approximately 75%, seemed to inhibit *B. edulis* (Salerni and Perini, 2004) and *Cantharellus formosus* production (Pilz et al., 2006). This negative effect of heavy thinning may be related to the twofold effect of an accelerated drying of forest soils and the mortality of many colonies of mycorrhizal fungi so that the net effect on mushroom yields is consistently negative. Bonet et al. (2012) also studied the effect of thinning intensity on mushroom yields in Mediterranean pine forests, and found that light thinning was more beneficial than heavy thinning in terms of the yields obtained for the target group of fungal species (*L. deliciosus s.l.*). Maximum mushroom yields were found when stand basal area removal was approximately 10 m^2 ha^{-1}. Conversely, heavy thinning can have negative effects on mushroom yields (Bonet et al., 2012).

3.2 Regeneration methods

Regeneration methods are harvesting techniques that aim to successfully establish a new cohort of trees that contributes to forest regeneration. Regeneration methods can be categorized into three main groups: clear-cutting, shelterwood methods and selective cuts. On the one hand, clear-cuts and shelterwood methods are typical of even-aged forestry, where successive thinnings may be combined during the rotation period with the possibility of performing a final cut in which the tree cover of adult trees is removed at the end of the rotation. On the other hand, selective cutting is the typical regeneration method in uneven-aged forests, also called continuous cover forestry, where tree cover is continuously maintained (Duryea and Dougherty, 2012; Pukkala and von Gadow, 2012).

Clear-cutting is a forestry practice in which all the trees of a given area are cut down. It has been reported to negatively influence the fruiting of most edible ectomycorrhizal fungi for approximately a decade until a new cohort of host trees establishes and their growth rate is sufficient to provide the ectomycorrhizal fungi with enough carbohydrates to support mushroom sporocarps (Kardell and Eriksson, 1987; Ohenoja, 1988; Durall et al., 2006). This effect has been reported even if the soil of a clear-cut area contains a quantity of potential inoculum similar to the adjacent forest area (Harvey et al., 1980; Le Tacon, 1997). Furthermore, Parladé et al. (2017) reported that clear-cutting also has a negative effect on the survival of mycelium in the soil. By contrast, Hintikka (1988) found that mushroom yields recovered in the first years after the regeneration cut, when young and vital specimens are growing. Clear-cutting is also widely used for coppice management. Lee et al. (2016) found that the presence of *Armillaria* spp. increased in the first seven years after clear-cutting mixed oak stands. This result depends on the ecology of *Armillaria mellea s.l.*, which includes both saprotrophic and pathogenic species that mainly infect trees with compromised physiology.

Shelterwood methods are another silvicultural option that can be used to enhance stand regeneration. They can be regarded as a progression of high-intensity thinning by preserving some standing, living, adult trees that will produce and spread seeds for the establishment of a new cohort of trees. Mushroom production by mycorrhizal fungi is higher in stands that were regenerated using shelterwood methods than in clear-cut stands because the remnant trees act as a fungal reservoir from which mycorrhizal fungi colonize the roots of the new cohort of trees (Peter et al., 2013). Similar results have been reported by Ágreda et al. (2014), who monitored fungal production in a cronosequence in *P. sylvestris* forests in Central Spain. They found that edible fungi were less abundant in the 10 years after shelterwood regenerative cuts. However, the presence of seed trees helped to support mushroom production. For this reason, the authors suggest the maintenance of seed trees as a relevant silvicultural tool to ensure the production of sporocarps and tree regeneration.

Selective cuts refer to small-scale forest management measures that aim to remove either single trees or small groups/patches of trees in order to facilitate regeneration in the resulting forest gap (Pukkala and Von Gadow, 2012). These operations have been found to influence fungal communities: the production of ectomycorrhizal mushrooms can be lower in the gap created by the selective cut compared to the surrounding uncut stands (Grebenc et al., 2009), particularly if all the trees in the gap are removed (De Groot et al., 2016).

However, the effect of regeneration cuts may differ among mushroom species, based on their ability to colonize a particular site after natural or man-induced disturbances. Fungi with resistant propagules or a high capacity for spore dispersal may rapidly colonize a site. Conversely, other species need an undamaged mycorrhizal network to connect them to the new host tree (Peter et al., 2013). Furthermore, differences in colonization ability are related to the different strategies used by fungi in the competition for water and nutrient uptake versus other fungal species.

3.3 Use of mycorrhized trees

Techniques for inoculating tree seedlings with ectomycorrhizal fungi have been widely studied; however, these studies have mainly focused on ectomycorrhizal fungi that promote tree growth and do not produce edible mushrooms or are not valued as food (Le Tacon et al., 1992; Savoie and Largetoie, 2011).

With regard to edible mushrooms, mycorrhized trees are successfully used to establish forest plantations for producing hypogeous edible fungi (truffles); however, these practices are more related to arboriculture than silviculture. Mycorrhized trees are not used to produce edible epigeous mushrooms in natural or planted forest ecosystems owing to a lack of evidence that this practice enhances the production of valuable ectomycorrhizal mushrooms. However, some promising results were observed by Martínez de Aragón et al. (2012) who tested the viability of introducing *Quercus ilex* seedlings inoculated with *Tuber melanosporum* (a hypogeous edible fungal species) into forest areas affected by large forest fires. The presence of the associated target mycorrhizae was observed in the seedlings ten years after planting. Unfortunately, no similar studies using wild edible epigeous mushrooms seem to have been performed.

Among the huge diversity of fungal species, only a small number of species have been domesticated. Currently, commercial nurseries offer a limited variety of mycorrhized plants inoculated with marketable fungal species, of which *Cantharellus cibarius*, *Tricholoma magnivelare*, *Boletus edulis* *s.l.* and *Lactarius delicious s.l.* are the most remarkable epigeous edible species, apart from the hypogeous fungi *Tuber melanosporum* and *Tuber aestivum*.

Some experimental plots with trees mycorrhized with *Cantharellus cibarius* were established in Sweden. The *C. cibarius* mycorrhiza survived transplantation and spread onto new roots but sporocarps did not form (Danell et al., 2002, Wang and Chen, 2014).

Plants mycorrhized with *Tricholoma matsutake* have been produced *in vitro*, and mycorrhizal formation *in situ* has also been reported (Wang et al., 1997; Yamada et al., 2006; Wang et al., 2012). More than 40,000 mycorrhized seedlings have been planted into existing *Pinus densiflora* forests in South Korea where *T. matsutake* is not currently present. However, there is no report of the progress of this experiment (Wang and Chen, 2014) and, to date, no other attempts to increase the production of this species in forests using this method have been reported.

With regard to *Boletus* species, mycorrhized plants have been produced under controlled conditions (Zuccherelli, 1988; Olivier et al., 1997). Some plantations have also been established in Mediterranean countries, such as Spain, where *Cistus* plants mycorrhized with *Boletus edulis* produced fruiting bodies three years after transplanting (Oria-de-Rueda et al., 2008), as well as in other small-scale experiments around the world (Wang and Chen, 2014). Recently, Mediavilla et al. (2016) observed that mycorrhization of *B. edulis* species could be improved using the helper bacteria *Pseudomonas fluorescens*.

The cultivation of *Lactarius* species has been widely studied since the 1980s because of their importance for recreational picking activities and as a commercial harvest. Poitou et al. (1984) reported the production of fruiting bodies in the field from outplanted *Pinus pinaster* mycorrhized seedlings. Guinberteau et al. (1990) reported that sporocarps develop 3 years after the seedlings establish. The *Lactarius deliciosus s.l.* species is also cultivated in French and Italian orchards, with up to 80 kg ha^{-1} harvested in the first years after transplanting (http://www.robinpepinieres.com). In

New Zealand, hundreds of hectares have been planted with trees inoculated with *L. deliciosus* over the past 10 years that produce fruiting bodies every year (Wang and Chen, 2014). For example, yields of 50 kg ha^{-1} of *L. deliciosus* in *P. pinaster* plantations have been reported (Wang and Hall, 2004), as well as yields of *Lactarius* spp. of approximately 300 kg ha^{-1} in 3-year-old *Pinus radiata* plantations in New Zealand (Guerin-Laguette et al., 2014). However, even for *Boletus* and *Lactarius* species, positive results are reported only for orchards and plantations on bare soil. There is no scientific evidence that planting mycorrhized trees in a natural forest ecosystem enhances mushroom production.

Other measures aimed at increasing the abundance of mycorrhized trees in a forest involve directly inoculating the soil with spores or retaining mature sporocarps within the forest to act as a source of inoculum. These procedures have been used in Japan to increase the productivity of *T. matsutake* (Wang and Hall, 2004). Similar measures have been employed in South Korea and China (Wang and Hall, 2004). In China, e.g., the yield of *Lactarius volemus* sporocarps increased in areas with mature pine trees inoculated with spores of this species (Liu et al., 2007). However, there is not a convincing body of evidence that infecting trees with target fungi at the time of planting or directly in the field within the first months after planting leads to infection and colonization (Duñabeitia et al., 2004). Indeed, plant inoculation with edible mycorrhizal mushrooms is mostly conducted using *in vitro* and greenhouse techniques.

3.4 Other management practices and disturbances

In addition to the above-mentioned stand characteristics and silvicultural treatments influencing fungal fruiting and/or contributing to changes in mycocenoses, additional human interventions related to forest management may also affect productivity, i.e., timber harvesting operations, mushroom picking activities, trampling, disturbance of woody debris and fire (including both wildfire and prescribed burning).

3.4.1. Timber harvest and detrimental soil disturbance

Timber harvesting is one of the operations that may have a great influence on mushroom occurrence immediately after thinning or regeneration cuts. It is well known that the physical properties of the soil can be significantly affected by harvesting operations, depending on the load of the machinery and the frequency of passes (Picchio et al., 2012). Soil compaction caused by logging techniques results in a critical reduction of water retention capacity, thus negatively influencing the long-term dynamics and fruiting of ectomycorrhizal fungi such as *Cantharellus* spp. (Amaranthus et al., 1996). Therefore, the potential impact on soil compaction should be considered when planning thinning or regeneration cuts. In this regard, although frequent and light forest interventions may be preferable to support mushroom yield (Pilz and Molina, 2002), frequent harvesting operations may also result in greater soil compaction than infrequent heavy felling (Amaranthus et al., 1996).

Mushroom-oriented silviculture should therefore implement harvesting methods and procedures with the aim of preserving forest soils. Indeed, the use of low-impact harvesting procedures may reduce the negative effects of logging, and mycosilvicultural interventions may even generate positive effects by increasing the productivity of some target mushroom species (Bonet et al., 2012). For instance, motor-manual felling and the extraction of whole trees by yarder would be preferable to using heavy machinery or winching and skidding methods because the impact on soil compaction is minimal. If this procedure is not applicable or convenient, appropriate training, the use of directional felling and careful supervision are necessary to minimize harvesting impacts on forest soils (Marchi et al., 2014).

3.4.2. Mushroom picking

Because of the increasing harvesting pressure in many parts of the world (Boa, 2004), a widespread concern about overharvesting and possible damage to fungal resources has been raised (Egli et al., 2006). Legal restrictions on the harvesting of edible fungi have been introduced in many countries because there is a fear that sporocarp removal, which often occurs before spore dispersal, might impair reproduction. Two experiments conducted in Oregon (Norvell, 1995) and Switzerland (Egli et al., 1990; Egli et al., 2006) found that sporocarp yield was not related to levels of mushroom harvesting. In a recent study, Parladé et al. (2017) also found that intensive picking did not significantly affect the mycelial biomass of *Boletus edulis* in the soil.

The Oregon Mycological Society Chanterelle Study evaluated the effect of mushroom harvesting, including the impact of different harvesting methods (i.e., either pulling up or cutting), and found no significant productivity decline in the first 10 years since the start of the study (Norvell, 1995). Egli et al. (2006) also investigated whether the mushroom harvesting technique affected mushroom production. They found that systematic harvesting did not reduce future yields of sporocarps. Similar results have also been reported for specific mushroom species such as *Tricholoma magnivelare* (Luoma et al., 2006) and *Morchella* spp. (Pilz et al., 2004; Larson et al., 2016).

However, although mushroom harvesting does not appear to affect fruitbody production *per se*, trampling caused by successive mushroom pickers throughout a given forest area may negatively affect fruitbody production. Sporocarp abundance in trampled areas can be 70% lower than in untrampled sites according to Egli and Ayer (1997) and Egli et al. (2006). However, there is no evidence that trampling affects the abundance of soil mycelia. The authors suggested that trampling possibly damages the sporocarp primordia (Egli and Ayer, 1997). Another hypothesis is that the reduction in yield may be linked to a decrease in the water retention capacity in the upper soil layers due to soil compaction. However, some fungal species (e.g., *Morchella* species) are often observed to fruit more abundantly on disturbed or compacted forest soils. Thus, mushroom pickers seeking morels tend to follow paths of logging equipment to search for concentrations of morels, which sometimes fruit on the footprints of previous mushroom harvesters (Pilz et al., 2006).

3.4.3. Removal of forest litter

Another disturbance that has been evaluated with regard to its effect on wild mushroom production is raking, i.e., the removal of forest litter. Several authors, such as Baar and Kuyper (1993) and Baar and Ter Braak (1996), have reported that mushroom production by mycorrhizal species in *Pinus sylvestris* stands increases as a result of litter removal, especially two years after litter removal. By contrast, Salerni and Perini (2004) reported that manual removal of the litter layer negatively affected the fruiting process of *Boletus edulis* in silver fir forests in Central Italy. These contrasting results may be because the fungal response to raking is species specific; however, as yet the effects of this operation are not well known.

3.4.4. Removal of understory vegetation and shrub control

The aim of shrub control is to increase (i) the survival and growth rate of mycorrhized trees by reducing competition for water and nutrients and (ii) the proliferation of mycelium as a consequence of improving the growth conditions of the host trees'.

The removal of understory vegetation may have an influence on mushroom production in forest ecosystems. An experiment conducted in central Italy (Tuscany) on Turkey oak (*Quercus cerris*) stands between 2000 and 2002 reported that the yield of *Boletus aereus* increased after removing the shrub layer growing under the oak canopy (Nocentini et al., 2004). The authors suggested that the increase in yield was a consequence of the ecology of the species, i.e., *B. aereus* being a termophilous species would benefit from the increased sunlight reaching the soil.

However, shrub vegetation itself can also be very productive in terms of mushrooms. For instance, *Cistus* scrublands can provide high yields of valuable, edible mushroom species, including *Boletus edulis* (Hernández-Rodríguez et al., 2015a, 2015b). In this regard, shrubs may play an important role in mushroom-oriented silviculture inasmuch as they may act as an accompanying species/reservoir, hosting fungal species that may inoculate new trees emerging after thinning or regeneration cuts. Another potential use of shrubs is the restoration of non-productive, degraded land where trees are not able to grow in order to obtain the joint benefits of soil protection (e.g., to reduce further soil erosion and degradation) and the production of highly valuable non-wood forest products such as mushrooms (Hernández-Rodríguez et al., 2013).

3.4.5. Prescribed burning

Prescribed burning is a management practice that aims to remove deadwood and other fuel biomass with the main objective of reducing the fire risk. In some cases, this practice can enhance the production of certain mushroom species that benefit from major disturbances such as wildfires. For example, Pilz et al. (2004) found that some putative species belonging to the genus *Morchella* (identified by molecular techniques among harvested black morels) fruited on burned areas. Winder and Keefer (2008) found that the average morel production after fire is about 6,500 morels ha^{-1}. However, where the level of duff consumption reached 71%, morel abundance increased up to 16,827 morels ha^{-1}.

In a more recent study, Larson et al. (2016) assessed post-fire morel abundance in a mixed coniferous forest and estimated an average yield of approximately 1,700 morels ha^{-1} in the first year following a fire. Moreover, they also demonstrated that additional key factors controlling post-fire morel production vary at small spatial scales, resulting in the spatial patchiness of morel distribution. However, not all *Morchella* species are fire-prone (Pilz et al., 2004). While sporocarp formation of some *Morchella* species is influenced solely by temperature and precipitation during springtime (Mihail et al., 2007), other species require an additional forest disturbance, including fire (Pilz et al., 2004; Wurtz et al., 2005). Furthermore, Pilz et al. (2007) suggest that morels can behave either as saprotrophic or mycorrhizal fungi at different stages of their life cycle.

Martín-Pinto et al. (2006) assessed the effect of wildfire on mushroom production in scrublands (dominated by *Cistus ladanifer*) and *Pinus pinaster* stands in central Spain. They observed an increase in sporocarp yield of pyrophytic mycorrhizal species (e.g., *Leccinum corsicum*), whereas *Boletus* *edulis* was not found in burned plots. More recently, Hernández-Rodríguez et al. (2015a) evaluated the effect of fire on fungal production in *C. ladanifer* scrublands by comparing the effects of total burning versus total clearing of the vegetation. In the first years after treatment, they found that mushroom production by mycorrhizal fungi was significantly higher after total clearing as compared to total burning. The authors suggest that if the primary objective is to increase the economic profitability of *C. ladanifer* scrublands, total clearing may be a preferable management option in order to enhance the yield of valuable, edible mushrooms.

3.4.6. Absence of forest management

In the long term, if no management practices are performed, stands may gradually evolve into old-growth forests. Unmanaged old-growth forests differ from managed stands because the life cycle of trees is not interrupted and natural dynamics resulting after disturbances (e.g., parasite outbreaks, forest fires and heavy windstorms, gap creation due to insects, fungal decay and windstorms) are not controlled by forest management (Heilmann-Clausen et al., 2017). From a structural point of view, old-growth forests differ from mature managed forests in terms of the amount of living biomass and in the richness and abundance of dead wood habitats.

Very few studies have evaluated mushroom yields in old-growth forests. Smith et al. (2002) observed very low sporocarp yields in old-growth *Pseudotsuga menziesii* forest stands, especially when compared to managed stands. Furthermore, edible species such as *L. deliciosus* were absent from old-growth forests that were more than 400 years old (Smith et al., 2002), which may be because this early-seral mushroom species prefers younger and rather open stands (Martínez-Peña et al., 2012a).

4. Conclusions and future perspectives

4.1 Current mycosilvicultural knowledge

Effective mycosilviculture for the production of edible mushrooms in forests should carefully take into account the variables affecting mushroom yield. Although the weather conditions largely drive mushroom yields (Alday et al., 2017a, 2017b), stand characteristics can also influence fungal resources. (i) Yields of mycorrhizal fungi are dependent on forest age, as more abundant sporocarps are generally observed in younger stands, which have a higher growth rate than trees in older stands. (ii) Canopy cover affects fungal yields: important edible and marketable species (*L. deliciosus*) benefit from stands with open canopies. However, in very open stands, productivity is lower than in less open stands. (iii) Stand density is one of the variables that influences mushroom production. Suitable stand basal areas for mushroom production depend on forest ecosystems and fungal species. In pine ecosystems, stand basal areas close to 20 m^2 ha^{-1} and 40 m^2 ha^{-1} are optimal for *Lactarius deliciosus s.l.* and *Boletus edulis s.l.*, respectively. (iv) Tree composition influences fungal communities due to the preference of some ectomycorrhizal and saprotrophic fungi for specific host trees or litter, respectively.

Forest management practices affect mushroom occurrence and production both positively and negatively (Figure 2). The main findings from the reviewed literature can be summarized as follows:

(i) The effect of thinning on fungal production is the most studied silvicultural practice. However, the effect of thinning on mushroom yield may be different for different fungal species. Several authors have found that thinning, particularly in coniferous stands, has a positive effect on the sporocarp yield of important marketable species (*Lactarius* spp., *Boletus* spp.) if it creates low-medium density stands. By contrast, a negative effect of thinning has been reported for target species such as *Cantharellus* spp., and high-intensity thinning can also lead to a reduction in sporocarp yield.

(ii) At least in the short-term, clear-cutting negatively affects mushroom production, mainly of mycorrhizal fungi. If several mature trees are kept within the stand as retention trees, the negative effect of this treatment could be reduced. For this reason, shelterwood methods may be preferable to support mushroom production during the regeneration period in even-aged stands.

(iii) The use of mycorrhized seedlings seems to be a promising way of increasing fungal production, especially after clear-cutting. However, while many positive results have been reported for greenhouse or plantation experiments, there is no clear scientific evidence that successfully transplanting mycorrhized plants in natural forests enhances mushroom production.

(iv) Due to soil compaction, logging negatively affects mushroom occurrence, especially if timber harvesting procedures are repeated frequently on the same site. Low-impact harvesting methods coupled with careful supervision are needed to minimize the impact of these operations on mushroom communities.

(v) Harvesting sporocarps does not have a direct impact on fungal yield, unless the ground is excessively trampled by mushroom pickers, which can result in a decrease in sporocarp yield. Further research is needed on the effects of trampling in areas visited by huge numbers of mushroom pickers to ensure the long-term provision of mushroom-based ecosystem services.

(vi) The impact of litter removal remains unclear: some studies have reported negative effects on the productivity of important marketable species (*Boletus edulis*), while other authors have reported the opposite trend for mycorrhizal species.

(vii) Fire can reduce mushroom production even more than clear-cutting. Exceptions are pyrophytic species, including, e.g., some strains of *Morchella* spp.

(FIGURE 2 HERE)

4.2 Gaps in knowledge and research needs

In this review we have summarized our current understanding of mushroom production and examined the main silvicultural effects that influence productivity (Table 2). We have identified several gaps in knowledge that require further research, which can be summarized in the following points.

(TABLE 2 HERE)

(i) Stand age is an important factor that can affect the mushroom production of socially and economically important fungal species (Bonet et al., 2004). However, there is a considerable gap in our knowledge concerning the influence of tree age distribution within the stand. Most studies conducted to date have focused on even-aged forest stands and, therefore, the whether there are differences in the productivity levels of even-aged and uneven- or multi-aged stands of a given forest ecosystem remains unclear. Given that most trees in uneven-aged stands belong to the younger age classes, such stands might benefit from the joint production of early- and late-successional fungi simultaneously, but further research is required to test this and alternative hypotheses.

(ii) Several studies have investigated the effect of silvicultural practices and logging operations in the first years after the intervention, but the long-term effect has not been fully explored. Further research should be devoted to understanding the recovery time of mushroom resources after different silvicultural operations (e.g., thinning or regeneration cuts). Moreover, further research on low-impact harvesting procedures in relation to wild epigeous mushrooms is also needed.

(iii) Most of the studies conducted to date have focused on sporocarp yield; however, a more comprehensive picture could be obtained if the abundance of mycelium in the soil was also taken into account (Liu et al., 2016; Parladé et al., 2017). Indeed, the disappearance of some species after logging may not be definitive, but simply relate to the new microclimatic conditions at soil level.

(iv) Most research conducted to date has focused on a few coniferous forest ecosystems (mainly *Pinus*-dominated stands). Less is known about other coniferous ecosystems (e.g. *Abies*-, *Larix*- and *Pseudotsuga*-dominated stands), particularly broadleaved forests such as beech, chestnut or oak forests. Deciduous forests are very important for mushroom picking activities in many regions, such as in temperate ecosystems and Mediterranean climates.

(v) To our knowledge, to date, no studies have been devoted to assessing the influence of tree species diversity on mushroom production. In particular, further research is needed to evaluate differences in fungal yield under pure and mixed forest ecosystems.

(vi) A comparison of the mushroom yields obtained under different silvicultural regimes is needed to verify, e.g., whether even-aged management regimes are better than uneven-aged ones or if coppice is preferable to high forest in broadleaved stands. This information would help managers to determine whether maintaining coppices or converting to high forest is the best option for mushroom yields and wood production.

(vii) The use of mycorrhized shrubs to restore degraded lands where trees are not able to grow may have promise as a way of increasing the value of degraded lands. However, to date, only a few studies have been carried out and further research is needed to provide further scientific evidence for different scrubland ecosystems.

(viii) Old-growth forests are considered to be an important resource that needs to be preserved, especially their role in biodiversity conservation. However, little is known about mushroom yields in old growth forests.

(ix) Most mycosilvicultural research studies have been conducted in Europe and North America, focusing on Mediterranean, temperate and boreal ecosystems. Our scientific understanding of mycosilviculture in other regions of the world and in other forest ecosystems and biomes (e.g., tropical) is still very limited.

(x) Models to predict mushroom yields have been proposed for relevant marketable species (e.g., *Boletus* spp. and *Lactarius* spp.); however, their validity is still local or regional. Silvicultural models that correlate arboreal carbon allocation with stand conditions and management regimes are available (e.g., Landsberg et al., 2003) and may be applied to model the production of forest mushrooms in order to provide more dynamic and efficient estimates of mushroom yields.

(xi) The context of global change should also be considered in future research. In particular, we need to determine how changes in precipitation and temperature patterns associated to climate change as well as global perturbations in the C and N cycles (increased CO_2 in the atmosphere; nitrogen deposition) will affect mushroom fruiting (Pickles et al., 2012; Suz et al., 2014). Furthermore, the predicted vegetation shifts, which may result in changes (i.e., migration) of host tree species of valuable fungi, should be also taken into consideration when modelling future mushroom yield scenarios.

In summary, a better understanding of the effect of forest management practices on mushroom production should provide a basis for improving productivity in forest stands. The research lines outlined above should not only enable us to acquire an in-depth ecological knowledge of forest ecosystems and fungal dynamics but also provide valuable scientific knowledge to support decision-making in forest management planning and policy-making (Corona, 2014; Corona et al., 2016).

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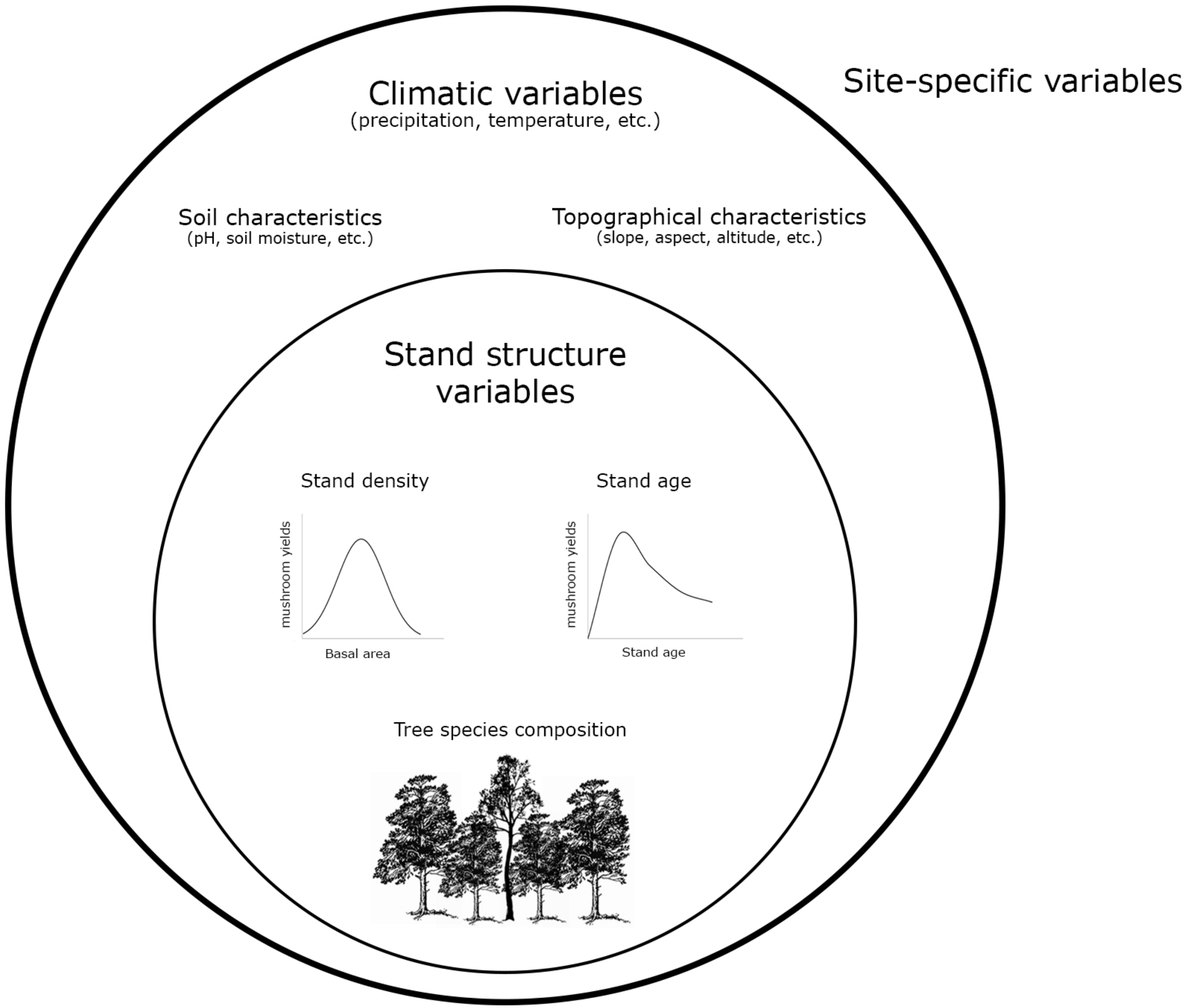
Figure 1. Site-specific variables influencing mushroom yield. The inner circle denotes drivers typically modified through silviculture and forest management.

Figure 2. Effect of silvicultural operations and forest management practices on mushroom yield.


Site-specific variables
Climatic variables
(precipitation, temperature, etc.)
Soil characteristics
(pH, soil moisture, etc.)
Topographical characteristics
(slope, aspect, altitude, etc.)
Stand structure variables
Stand density
mushroom yields
Basal area
Stand age
mushroom yields
Stand age
Tree species composition

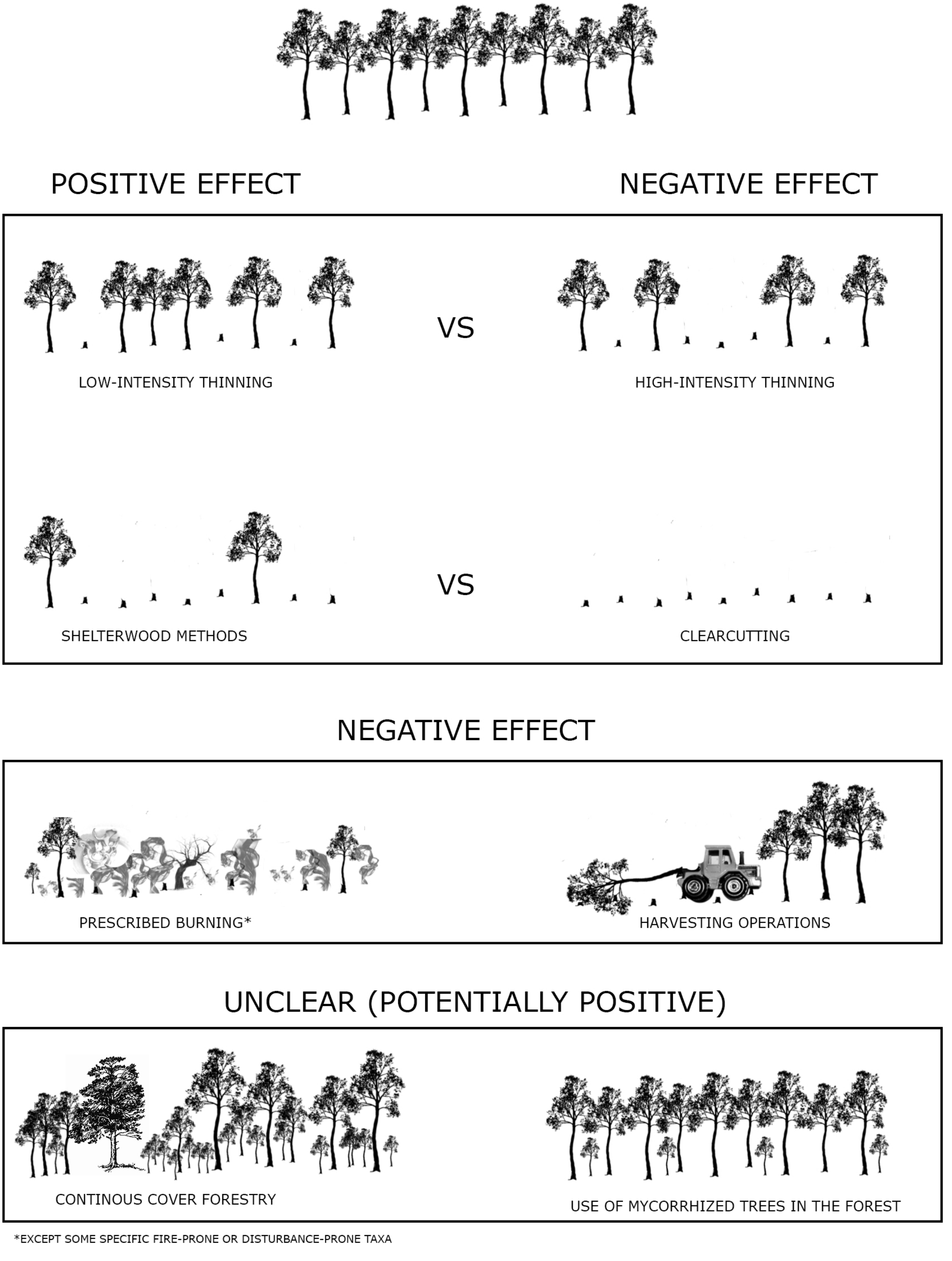

POSITIVE EFFECT
NEGATIVE EFFECT
VS
LOW-INTENSITY THINNING
HIGH-INTENSITY THINNING
VS
SHELTERWOOD METHODS
CLEARCUTTING
NEGATIVE EFFECT
PRESCRIBED BURNING*
HARVESTING OPERATIONS
UNCLEAR (POTENTIALLY POSITIVE)
CONTINOUS COVER FORESTRY
USE OF MYCORRHIZED TREES IN THE FOREST
*EXCEPT SOME SPECIFIC FIRE-PRONE OR DISTURBANCE-PRONE TAXA

Table 1 Wild epigeous edible mushroom species considered in this review as relevant for mycosilviculture focused on the supply of food provisioning ecosystem services further linked to provision of cultural ecosystems services (e.g., recreation and tourism) and commercial relevance.

Life form	Family	Species	Associated tree/shrub species*	References
ectomycorrhizal	*Russulaceae*	*Lactarius deliciosus s.l. (Lactarius deliciosus; Lactarius sanguifluus; Lactarius vinosus; Lactarius semisanguifluus)*	*Pinus sylvestris, Pinus nigra, Pinus halepensis, Pinus pinaster, Pinus contorta, Pinus radiata, Pseudotsuga menziesii*	Guinberteau et al., 1990; Smith et al., 2002; Martínez de Aragón et al., 2007; Ortega-Martínez et al., 2011; Bonet et al., 2012; Martínez-Peña et al., 2012a; Martínez-Peña et al., 2012b; Ágreda et al., 2014; de-Miguel et al., 2014; Guerin-Laguette et al. 2014; Kucuker and Baskent, 2015; Liu et al., 2016
		Lactarius deterrimus	*Picea spp.*	Buée et al., 2011
		Lactarius salmonicolor	*Abies alba, Abies bormülleriana*	Courtecuisse and Duhem, 1994; Kucuker and Baskent, 2015
		Lactarius volemus	*Pinus spp.*	Liu et al., 2007
	Boletaceae	*Boletus edulis s.l. (Boletus aestivalis, Boletus aereus, Boletus edulis, Boletus pinophilus)*	*Abies alba, Cistus ladanifer, Quercus spp., Picea spp., Pinus sylvestris*	Nocentini et al., 2004; Salerni and Perini, 2004; Oria-de-Rueda et al., 2008; Ortega-Martínez et al., 2011; Martínez-Peña et al., 2012b; de-Miguel et al., 2014; Hernández-Rodríguez et al., 2015a, Hernández-Rodríguez et al., 2015b; Mediavilla et al., 2016; Tahvanainen et al., 2016; Parladé et al. 2017
		Suillus granulatus	*Pinus spp.*	Savoie and Largetau, 2011

		Suillus bovinus	*Pinus sylvestris*	Shaw et al., 2003
		Suillus brevipes, Suillus tomentosus	*Pinus contorta*	Kropp and Albee, 1996
		Leccinum corsicum	*Cistus ladanifer*	Martín-Pinto et al., 2006
	Tricholomataceae	*Tricholoma magnivelare,*	*Abies amabilis, Abies magnfica var. shastensis, Pinus contorta, Pinus monticola, Pseudotsuga menziesii, Tsuga heterophylla, Tsuga mertensiana*	Weigand, 1997, Kranabetter et al., 2002; Kranabetter et al., 2005; Luoma et al., 2006;
		Tricholoma matsutake	*Pinus densiflora*	Wang et al., 1997; Wang and Hall, 2004; Wang et al., 2012; Wang and Chen, 2014; Yamada et al., 2006
	Cantharellaceae	*Cantharellus cibarius*	*Picea excelsa*	Danell et al., 2002, Wang and Chen, 2014
		Cantharellus formosus	*Picea sitchensis, Pseudotsuga menziesii, Tsuga heterophylla*	Kranabetter et al. 2009; Pilz et al. 2006
saprotrophic and ectomycorrhizal**	*Morchellaceae*	*Morchella spp. (Morchella conica s.l.; Morchella esculenta s.l.)*	*Abies concolor, Abies grandis, Abies lasiocarpa, Asimina triloba, Larix occidentalis, Picea glauca, Pinus contorta, Pinus lambertiana, Pinus ponderosa, Pseudotsuga menziesii,Tilia Americana, Ulmus americana*	Pilz et al., 2004; Mihail et al., 2007; Pilz et al., 2007; Winder and Keefer, 2008; Larson et al., 2016
saprotrophic and parasitic	*Physalacriaceae*	*Armillaria mellea s.l. (Armillaria mellea, Armillaria borealis, Armillaria cepistipes, Armillaria gallica,*	*Abies grandis, Clintonia uniflora, Physocarpus malvaceus, Quercus spp., Thuja plicata, Tsuga heterophylla*	Kim et al., 2010; Lee et al., 2016

		Armillaria ostoyae, Armillaria tabescens)		

* the species listed here are those characterizing study areas of cited mycosilviculture researches

** Morchella spp. can behave either as saprotrophic or mycorrhizal at different stages of their life cycle (Pilz et al., 2007).

Table 2. State of knowledge about major research topics examined in the present review concerning relationship between forest stand attributes, forest management practices, main disturbances and mushroom occurrence. Symbols indicate current knowledge about the topic: “absence or very little knowledge present in the literature” (--); “little knowledge and few experiences present in the literature” (-); “several studies dealing with the topic, but further research is still needed” (+).

Forest stand age	Influence of forest stand age on wild mushroom production	+
	Mushroom production in even-aged forests	+
	Mushroom production in uneven-aged forests	-
Stand density	Relationship between basal area and wild mushroom production	+
	Relationship between n° of trees per hectare and wild mushroom production	-
	Relationship between canopy cover and wild mushroom production	+
Tree species composition	Influence of tree species composition and diversity on wild mushroom production	--
	Mushroom production in coniferous forests	+
	Mushroom production in broadleaved forests	-
Effect of forest management practices	Effect of thinning on wild mushrooms production in the short term	+
	Effect of thinning on wild mushrooms production in the long term	-
	Effect of clear-cuts on wild mushrooms production	+
	Effect of shelterwood methods on wild mushrooms production	-
	Effect of selective cutting on wild mushrooms production	-
	Use of mycorrhized trees for enhancing mushroom production in natural forest ecosystems	--
	Effect of timber harvesting on wild mushrooms production	-

	Effect of shrub control on wild mushrooms production	--
	Absence of forest management	--
Effect of other disturbances	Effect of picking activity on wild mushrooms production	+
	Effect of removal of litter on wild mushrooms production	-
	Effect of fire on wild mushrooms production	+